

New Records of Plio-Pleistocene Koalas from Australia: Palaeoecological and Taxonomic Implications

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ABSTRACT. Koalas (Phascolarctidae, Marsupialia) are generally rare components of the Australian fossil record. However, new specimens of fossil koalas were recovered during recent systematic excavations from several eastern Plio-Pleistocene deposits of Queensland, eastern Australia, including the regions of Chinchilla, Marmor and Mt. Etna. The new records are significant in that they extend the temporal and geographic range of Plio-Pleistocene koalas from southern and southeastern Australia, to northeastern central Queensland. We provide the first unambiguous evidence of koalas in the Pliocene Chinchilla Local Fauna (phascolarctid indet. and *Ph. ?stirtoni*): important additions to an increasingly diverse arboreal mammalian assemblage that also includes tree kangaroos. The persistence of koalas and local extinction of tree kangaroos in the Chinchilla region today suggests that significant habitat and faunal reorganization occurred between the Pliocene and Recent, presumably reflecting the expansion of open woodlands and grasslands. Other koala records from the newly U/Th-dated Middle Pleistocene Marmor and Mt. Etna fossil deposits (*Phascolarctos* sp. and *Ph. ?stirtoni*), along with independent palaeohabitat proxies, indicate the former presence of heterogeneous habitats comprised of rainforests, open woodlands and grasslands. The lack of such habitat mosaics in those regions today is likely the product of significant Middle Pleistocene climate change.

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Koalas (Phascolarctidae, Marsupialia) are Australian endemic, relatively large-sized (c. 10 kg), arboreal marsupials that occupy a similar ecological niche to placental lemuroids or sloths (Murray, 1984). The modern Koala, *Phascolarctos cinereus*, is the only surviving member of an ancient and diverse family of marsupials, with the oldest members known from the Late Oligocene (Black, 1999). Six to seven genera and 18 species (several undescribed) are currently recognized (Black, 1999). Phascolarctids are

separated from all other vombatiformes (i.e., wombats, marsupial “lions”, illarids, wynyardiids, maradids, and diprotodontoids) on the basis of their selenodont dental morphology and occupy a position near the base of the diprotodontian ordinal tree (Archer, 1976; Archer & Hand, 1987). A recent molecular phylogeny supermatrix, temporally-constrained using dated occurrences of fossil taxa, suggested that koalas diverged from vombatoids during the Middle Eocene (Beck, 2008).

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Koalas are generally rare components of the Australian fossil record, presumably reflecting their arboreal habits (Murray, 1991), and fossil koala material is commonly fragmentary and/or poorly preserved. Thus, determination of intra- and interfamilial phascolarctid relationships has proven difficult. Pre-Holocene koalas are known from Oligo-Miocene deposits of Riversleigh, Frome Basin, and Tirari Desert (Stirton *et al.*, 1967; Woodburne *et al.*, 1987; Black & Archer, 1997; Myers *et al.*, 2001; Louys *et al.*, 2007); Late Miocene-Pliocene deposits of Corra Lynn Cave and Waikerie (Pledge, 1987); and Pleistocene deposits of Koala Cave, Mammoth Cave, Devil's Lair, Tight Entrance Cave, Lake Eyre region, Madura Cave, Lake Menindee, Lake Victoria, Nelson Bay, Naracoorte region, Wellington Caves, and Gore (Bartholomai, 1968; Merrilees, 1968; Archer, 1972; Balme *et al.*, 1978; Lundelius & Turnbull, 1982; Tedford & Wells, 1990; Archer *et al.*, 1997; Dawson & Augee, 1997; Moriarty *et al.*, 2000; Reed & Bourne, 2000; Piper, 2005; Ayliffe *et al.*, 2008; Price, 2008a) (Fig. 1). The koala fossil record from the central to north eastern margin of the Australian continent is particularly depauperate, with only one specimen known (type specimen of *Phascolarctos stirtoni* from Gore, southeast Queensland). *Koobor*, a koala-like vombatiform marsupial is also known from isolated specimens from the Bluff Downs (central eastern Queensland) and Chinchilla Local Faunas (southeastern Queensland (Archer & Wade, 1976; Archer, 1977a). Although originally considered to be a koala, more recent morphology-based phylogenetic analyses suggest that *Koobor* sits outside the Phascolarctidae (Black & Archer, 1997) and may actually be a primitive sister-group of wynyardiids and ilariids (Myers & Archer, 1997).

Here we report new specimens of fossil koalas that were recovered during recent systematic excavations from several Plio-Pleistocene deposits of eastern Queensland, including the regions of Chinchilla, Marmor and Mt. Etna (Fig. 1). Although the new specimens are fragmentary, the paucity of information about koalas in the Plio-Pleistocene makes the new eastern Australian material particularly noteworthy. Thus, the aim of this paper is to describe the new material and discuss the taxonomic and palaeoecological implications within a reliable geochronological framework.

Materials and methods

Dating. Samples of bone and post-depositional calcite growth within long-bone hollows from the Marmor and Mt. Etna cave fossil deposits were targeted for thermal ionization mass spectrometry (TIMS) U/Th dating. Each sample was pre-treated and processed at the Radiogenic Isotope Facility, The University of Queensland, following techniques described in Zhao *et al.* (2001) and Yu *et al.* (2006).

Speleothem calcites and aragonites are secondary mineral deposits that form in cave environments. Uranium is commonly leached from downward percolating meteoric waters and becomes co-precipitated within speleothem calcite (or aragonite) during genesis. At the time of speleothem formation, some U, but little or no Th, is incorporated into the calcite (or aragonite) lattices, and disequilibrium in the U-series decay chain occurs. The U/Th age is calculated by determining the amount of ^{230}Th that was produced by the decay of ^{238}U (via intermediate isotope ^{234}U). Thus, dating of speleothem material provides

the true age of initial calcite crystallization. However, in this dating study, the calcite precipitated within long bone hollows at some stage after deposition, thus, the calculated U/Th ages will represent minimum ages for the associated faunal assemblages.

Fresh bone and teeth contains little or no U. However, after burial, U is taken up from the environment by bone apatites that scavenge U, but exclude Th, during diagenesis. Unlike speleothem, bones and teeth are open systems for U (Grün *et al.*, 2008), therefore, the U/Th dates commonly represent the mean age of U-uptake history. Thus, a calculated age most likely represents a minimum age for the dated bone or tooth. This has previously been demonstrated for eastern Australian cave deposits where U/Th dating of deposit-capping speleothem (thus, also representing minimum ages) return dates that are always older than U/Th dated bone and teeth recovered from within the deposit itself (Hocknull *et al.*, 2007).

Unfortunately, U/Th datable material that could potentially produce maximum ages of deposition was not recovered from the Marmor and Mt. Etna koala deposits. No dateable samples were obtained from the Chinchilla fossil deposits.

Terminology. Dental nomenclature follows Lockett (1993) where the adult unreduced cheek tooth formula of marsupials is P1–3 and M1–4 in both upper and lower dentitions. Dental cusp terminology follows Archer (1978) except for what was then interpreted to be the hypocone, is now regarded to be the metaconule, based on its linkage through the postprotocrista with the protocone and metacone (Tedford & Woodburne, 1987; Tedford & Woodburne, 1998). Higher-level systematic nomenclature follows Aplin & Archer (1987). All measurements were made using callipers and are given in millimetres (mm).

Institutional abbreviations. QMF, Queensland Museum Fossil specimen, Queensland Museum, Brisbane, Australia; QMJ, Queensland Museum modern specimen, Queensland Museum, Brisbane, Australia; QML, Queensland Museum fossil Locality, Queensland Museum, Brisbane, Australia; SAMP, South Australian Museum Palaeontological specimen, South Australian Museum, Adelaide, Australia.

Geographic and geological settings

Chinchilla. Site QML7 is located in Chinchilla, south-eastern Queensland (Fig. 1). Vertebrate fossils, constituting the Chinchilla Local Fauna, are predominantly derived from the Chinchilla Sand, a lithostratigraphic sequence of fluvial sediments exposed in the Condamine River between Nangram Lagoon and Warra (Woods, 1960). The Chinchilla Sand includes well-lithified calcareous sandstones grading into siltstone and conglomerate (quartz and ferruginous sandstone), and weakly consolidated sands that grade into silt and sandy clay. Such sediments were derived from erosion of the Orallo Formation and its lateritized profiles (Bartholomai & Woods, 1976). There are no analytical dates associated with the Chinchilla Sand. However, biochronological correlation based on fossil vertebrates to other important radiometrically-dated faunas from elsewhere in Australia (e.g., Kanunka Local Fauna,

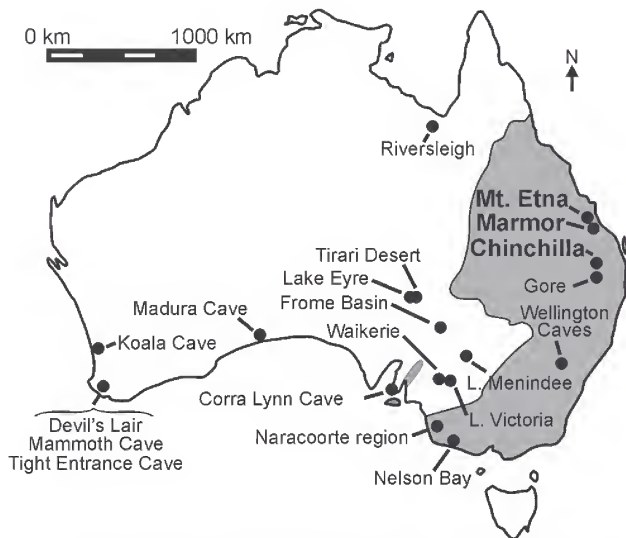


Fig. 1. Oligocene-Pleistocene fossil localities where koalas have been recovered, including present study sites (Chinchilla, Marmor and Mt. Etna). Shaded area indicates historic (i.e., post-European settlement in Australia) geographic range of the modern Koala, *Phascolarctos cinereus*.

Bluff Downs Local Fauna, and Hamilton Local Fauna), suggests a Middle Pliocene age (Whitelaw, 1991; Tedford *et al.*, 1992; Mackness *et al.*, 2000).

Marmor. Site QML1420 is located in Marmor, central eastern Queensland (Fig. 1). QML1420 is a brecciated limestone cave deposit, with sediments dominated by grey to brown clays and limestone clasts (Hocknull, 2005). The deposit contains typical Pleistocene megafauna including *Diprotodon optatum*, *Thylacoleo carnifex* and *Macropus giganteus titan* (Longman, 1925) (*D. optatum* and *M. g. titan* taxonomy up-dated following Price (2008b) and Dawson & Flannery (1985), respectively). Direct U/Th dating based on teeth from such taxa returned minimum ages of 122–154 ka (Table 1) suggesting that the assemblage is Middle Pleistocene or older. The assemblage lacks faunal elements typical of Pliocene assemblages and on the basis of biocorrelation to nearby well-dated deposits of the Mt. Etna region (Hocknull *et al.*, 2007), site QML1420 is unlikely to be older than Middle Pleistocene.

Mount Etna. Site QML1384 (Unit “L.U.”; Elephant Hole Cave) is located at Mt. Etna, central eastern Queensland (Fig. 1). It is a brecciated limestone cave deposit, with sediments dominated by red/yellow/grey clays with occasional gravel and cobbles (Hocknull, 2005). Direct U/Th dating based on a macropod bone provided an age of 267 ± 5.2 ka (Table 1). However, due to unknown rates of U uptake, the date should be regarded as a minimum age only. This interpretation is supported by U/Th dating of calcite recovered from the hollow of long bone, which returned an age of 331.6 ± 14 ka (Table 1). This age is likely to be closer to, but still younger than, the true age of the fossil assemblage. A maximum age has not been determined for QML1384 “L.U.”, but based on faunal similarities to other dated sequences in the region, the deposit is unlikely to be older than 500 ka (Hocknull *et al.*, 2007).

Systematic Palaeontology

Super cohort Marsupialia Cuvier, 1817

Order Diprotodontia Owen, 1866

Suborder Vombatiformes Woodburne, 1984

Infraorder Phascolarctomorpha Aplin & Archer, 1987

Family Phascolarctidae Owen, 1839

Phascolarctidae gen. et sp. indet.

Figs 2, 3A

Referred material. QMF52287, left dentary fragment, QML7, Chinchilla, southeast Queensland, Australia (Pliocene).

Description. Dentary fragment with horizontal ramus broken anterior to P_3 alveolus and posterior to M_3 alveolus; surface bone slightly root-etched; cheek teeth crowns missing, roots present, alveolar border broken buccally; ventral border slightly in-turned lingually; mental foramen anteroventral to P_3 anterior alveolus; posterior mental foramen well developed, ventral to position between posterior root of M_1 and anterior root of M_2 ; symphysis strongly fused, very deep, extended posteriorly to below posterior root of M_1 , kinked such that posteroventral border extends below ventral border of horizontal ramus, inclined posteriorly at posteroventral margin, inclined anteriorly at a low angle (35°); genial pit, c. 3 mm largest diameter, present at posterior ventral portion of symphysis, similar symmetrical but broken pit present on opposing dentary.

Remarks. The dentary fragment is considered to be adult based on the presence of well-developed P_3 and M_3 alveoli, and a strongly fused symphysis. The dentary resembles phascolarctids in general morphology. However, QMF52287 does not appear to be referable to any phascolarctid where the dentary is known. It differs from *Nimiokoala*, *Perikoala*, *Madakoala*, and *Phascolarctos cinereus* by: (a) being significantly more robust in terms of depth and width (Fig. 3A); (b) possessing a more anteriorly positioned posterior mental foramen; (c) having a straighter ventral border; and (d) by possessing a relatively deeper symphysis that has a lower anterior ascending angle. QMF52287 is more gracile in comparison to *Cundokoala yorkensis* (a genus that is questionably distinct from *Phascolarctos*; see Black, 1999) (Fig. 3A), but like *Ph. cinereus*, also differs from the former taxon in having a more anteriorly positioned posterior mental foramen, straighter ventral border, and deeper symphysis. The dentary of *Litokoala* is unknown, but on the basis of alveoli dimensions, is probably significantly smaller than QMF52287. QMF52287 differs from *Perikoala* and *Madakoala* in that the symphysis is more strongly fused, and the diastema is relatively longer. Well-developed symmetrical genial pits are present at the posteroventral base of the symphysis of QMF52287, but are not expressed as strongly in other koala genera. Well-developed genial pits occur in wombats such as *Vombatus*, but such pits are relatively larger, positioned relatively higher from the ventral border, and the pits commonly converge on each other on the left and right side of the symphyseal fusion forming a

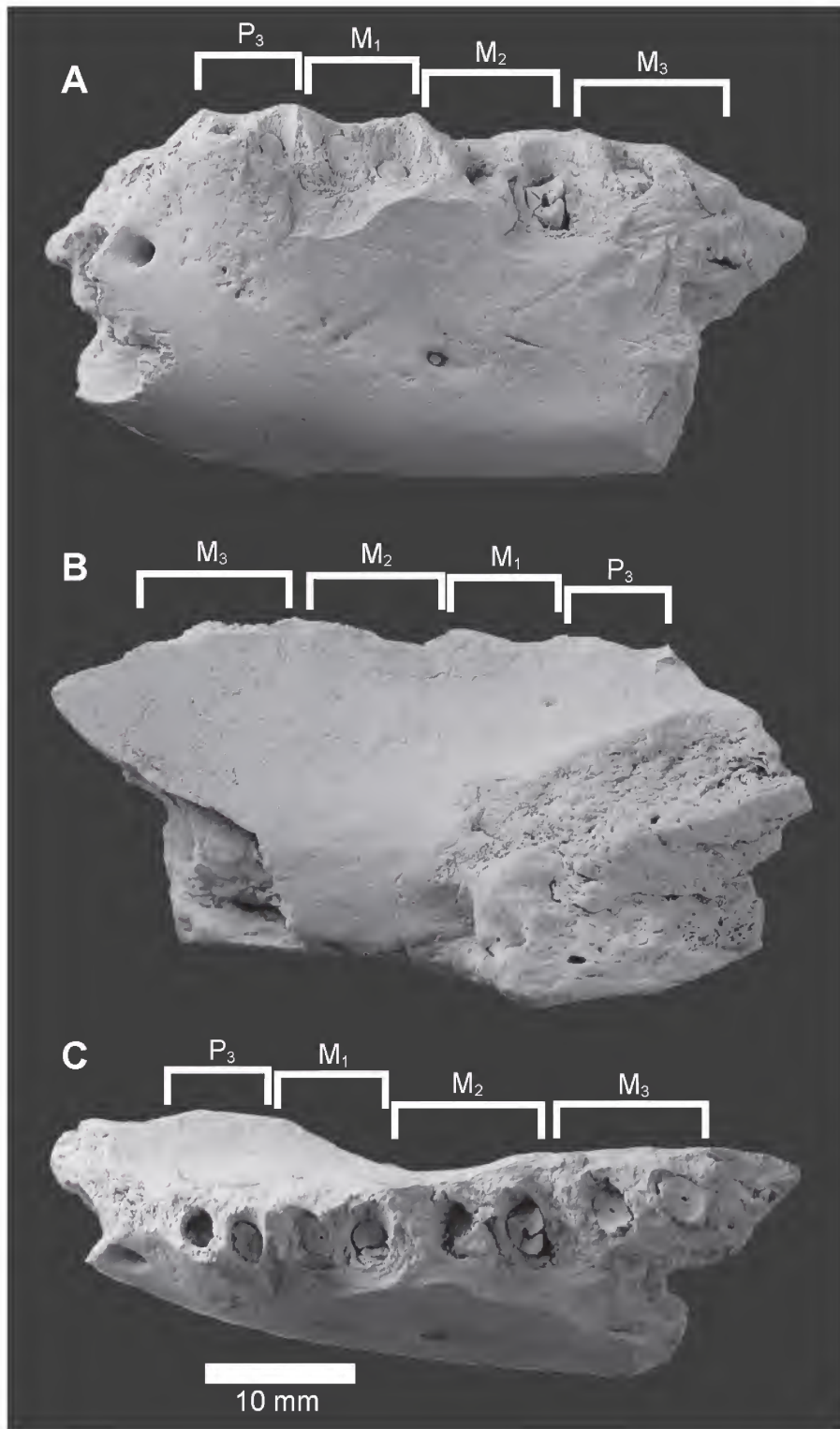


Fig. 2. Phascolarctid gen et sp. indet. dentary (QMF52287) from site QML7, Chinchilla, eastern Australia. (A) External view, (B) Internal view, and (C) Occlusal view.

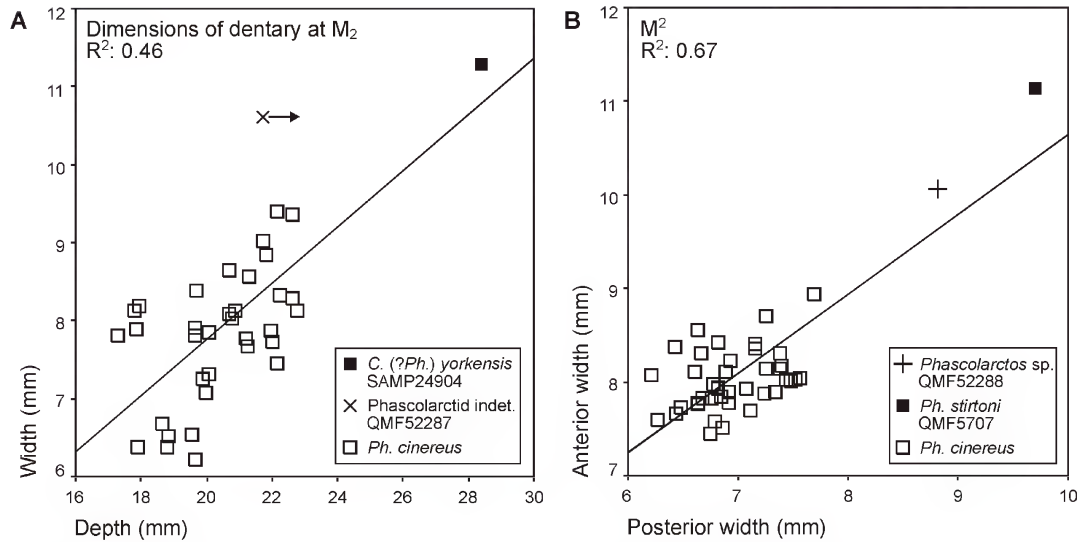


Fig. 3. Morphometrics of fossil koala specimens. (A) Depth versus width of dentaries of modern *Phascolarctos cinereus* from eastern Queensland (Appendix), fossil *Cundokoala* (?*Ph.*) *yorkensis* (SAMP24904) from Corra Lynn Cave (South Australia), and phascolarctid gen. et. sp. indet. (QMF52287) from Chinchilla, eastern Australia. Note that the depth of the Chinchilla koala dentary is a minimum measurement because the specimen is broken along the alveolar border (Fig. 2). (B) Anterior versus posterior width of *Phascolarctos* spp. M² (See Appendix for list of modern *Ph. cinereus* specimens examined).

Phascolarctos sp.

Figs 3B, 4A

single large pit. Comparison of QMF52287 to other large-sized phascolarctids such as *Ph. maris*, or unusual koala-like marsupials such as *Koobor*, is not possible because dentaries of those taxa are unknown.

Genus *Phascolarctos* Blainville (1816)

Diagnosis. Upper molars of *Phascolarctos* differ from all other phascolarctids (excepting *Cundokoala* (?*Ph.*) *yorkensis*) and the koala-like *Koobor* by: (a) being larger; (b) being relatively higher crowned; (c) by possessing well-developed molar crenulations; and (d) possessing well-developed ribs on lingual portion of paracone and metacone.

Phascolarctos differs from *Madakoala*, *Nimiokoala* and *Koobor* by possessing a lingual cingulum or pocket on upper molars at the crown base between the protocone and metaconule.

Phascolarctos differs from *Litokoala* and *Nimiokoala* by possessing relatively smaller neometaconules and paraconules.

Phascolarctos differs from *Madakoala*, *Perikoala*, *Cundokoala* and *Koobor* by possessing relatively smaller or weakly expressed stylar cusps, and in the case of *Cundokoala*, by possessing a relatively less-developed associated stylar shelf.

Phascolarctos differs from *Cundokoala* in being smaller and by possessing lesser-developed molar crenulations.

Phascolarctos differs from *Koobor* by: (a) having a square- to trapezoidal-shaped, rather than rectangular-shaped, occlusal outline; (b) possessing relatively longer anterior and posterior cingula; and (c) lacking a buccal ectoloph on the paracone.

Referred material. QMF52288, isolated LM², QML1384 (Unit “L.U.”; Elephant Hole Cave), Mt. Etna, central eastern Queensland, Australia (Middle Pleistocene; Table 1)

Description. LM² with anterior portion missing; tooth trapezoidal in occlusal outline, tapering posteriorly; protocone and paracone sub-equal in height, slightly taller than metacone and metaconule, neometaconule shortest cusp; protocone most anterior cusp forming anterolingual corner of tooth; paracone transverse, slightly posterior to protocone, forming anterobuccal margin of tooth; metacone directly posterior to paracone forming posterobuccal corner of tooth; metaconule posterobuccal to protocone, transverse to metacone, forming posterolingual corner of tooth; postprotocrista well developed, descends posterobuccally from apex of protocone to meet with premetaconulecrista; cristae on paracone missing; rib descends posteriorly from apex of paracone to mid-crown basin; premetacrista well developed, descends anterobuccally from apex of metacone, terminating at stylar cusp D; postmetacrista well defined, descends posterobuccally from apex of metacone; posterolingual crista weakly-expressed descending from metacone apex to posterolingual base of metacone; neometaconule small, distinct at anterolingual base of metacone; premetaconulecrista well developed, descends anterobuccally from apex of metaconule terminating at mid-crown basin; postmetaconulecrista well developed, descends posterobuccally from apex of metaconule, with inflexion at posterior cingulum; lingual cingulum moderately developed at base of crown between protocone and metaconule; posterior cingulum well defined, descends from inflexion with postmetaconulecrista, terminating at posterobuccal corner of tooth near stylar cusp E; metacone

buccal ridge small, descends posteriorly from stylar cusp D, terminating at posterobuccal corner of tooth; molar enamel heavily crenulated.

Remarks. QMF52288 is regarded as an M^2 due to its trapezoidal occlusal outline that tapers posteriorly and by its possession of a relatively small neometaconule, identical to that of M^2 in other species of *Phascolarctos*. QMF52288 is significantly larger than corresponding teeth of *Koobor*, *Madakoala*, *Perikoala*, *Nimiokoala* and *Litokoala*, and *Ph. cinereus*. However, the tooth is morphologically similar to other species of *Phascolarctos*. In comparison to *Ph. stirtoni*, the posterior cingula is relatively smaller, molar enamel is less crenulated (although that feature may be slightly variable judging from variation expressed in large samples of modern *Ph. cinereus*), and the tooth is smaller overall (Fig. 3B). However, judging by the range of morphometrical variation exhibited in modern *Ph. cinereus* (Fig. 3B), QMF52288 could easily fall within the lower size range of *Ph. stirtoni*. QMF52288 is somewhat similar in morphology to extant *Ph. cinereus*. However, it is larger and falls outside the morphometrical range of variation of modern populations (Fig. 3B). Pledge (1987) suggested that *Ph. maris* (a species questionable distinct from *Ph. stirtoni*; see Black, 1999) is intermediate in size between the smaller *Ph. cinereus* and larger *Ph. stirtoni*. Thus, QMF52288 potentially represents *Ph. maris*. However, it is not possible to compare QMF52288 to *Ph. maris* (nor to the significantly larger *Cundokoala* (?*Ph.*) *yorkensis*) as corresponding teeth are unknown in those species.

Phascolarctos stirtoni Bartholomai, 1968

Holotype. QMF5707, right maxillary fragment with P^3 , M^{1-2} , Cement Mills, Gore, southeastern Queensland (Late Pleistocene; Price *et al.*, 2009).

Diagnosis. See Bartholomai (1968).

Phascolarctos ?*stirtoni*

Figs 4B, C

Referred material. QMF52289, isolated $RM^{1.2 \text{ or } 3}$ fragment, QML7, Chinchilla, southeast Queensland, Australia (Middle Pliocene); QMF52290 isolated RM^2 fragment, QML1420 Marmor Quarry, central eastern Queensland, Australia (Middle Pleistocene; Table 1).

Description. $RM^{1.2 \text{ or } 3}$, description based on QMF52289: Metacone only major cusp preserved, very large, worn; postmetacrista moderately developed, descends apex of metacone posterobuccally to small stylar cusp E; buccal crest small but distinct, directed anteriorly from stylar cusp E, slightly ascending buccal margin of tooth; posterior cingulum large, worn; molar enamel crenulated at posterolingual base of metacone.

RM^2 , description based on QMF52290: Protocone only major cusp preserved; preprotocrista well developed, descends anterobuccally to lingual portion of anterior cingulum; postprotocrista descends posterobuccally to base of protocone; rib descends protocone between pre- and postprotocristae, well developed; anterior fossette well developed at anterior base of protocone; lingual cingulum

well developed, extending along lingual margin at base of protocone, ascending and terminating at lingual corner of tooth; molar enamel crenulated on all sides of protocone.

Remarks. The wear pattern on the posterior margin of the metacone molar fragment (QMF52289) is consistent with wear from abrasion with a succeeding tooth whilst still in the maxilla. This suggests that the specimen represents either an $M^{1.2}$ or M^3 , rather than an M^4 (the most posterior tooth in phascolarctids). On the basis of molar morphology, the teeth are referable to *Phascolarctos* due to: (a) their well-developed molar crenulations; (b) minor degree of development of stylar cusps and associated stylar shelf (QMF52289); (c) well-developed lingual cingulum (QMF52290); and (d) being higher-crowned than all other phascolarctids (excepting *Cundokoala* (?*Ph.*) *yorkensis*). Morphometrically, both teeth are larger than corresponding teeth of *Ph. cinereus*, but are smaller than corresponding teeth of *C. (?Ph.) yorkensis*. The protocone fragment (QMF52290) is morphologically similar to the corresponding M^2 of *Ph. stirtoni*, particularly in the development of the anterior fossette at the base of the protocone, and the anterolingual extension of the lingual cingulum. The metacone fragment (QMF52289) lacks a well-developed stylar shelf as exhibited in *C. (?Ph.) yorkensis*, and in that respect, closely resembles the condition exhibited in *Ph. stirtoni*. Corresponding teeth of *Ph. maris* and *C. (?Ph.) yorkensis* are either not known or are poorly represented, thus, preventing further comparison to the material described here. However, the molar fragments described here are similar in size to *Ph. stirtoni*, a species that is intermediate in size between *Ph. maris* and *C. (?Ph.) yorkensis* (Pledge, 1987, 1992). Thus, QMF52289 and QMF52290 are unlikely to be referable to those poorly known taxa. The fragmentary nature of the material precludes additional comparison to *Ph. stirtoni*.

Discussion

New koala material described here significantly extends the temporal and spatial distribution of Plio-Pleistocene koalas in Australia. Previously, Pliocene records of koalas were restricted to southern Australian deposits (i.e., Corra Lynn Cave and Waikerie). Thus, the new records from the Chinchilla Local Fauna (phascolarctid indet. and *Phascolarctos* ?*stirtoni*) represent a significant north-eastern geographic extension for Pliocene koalas, and provide the first unambiguous evidence for the presence of koalas in the assemblage. Similarly, new records of *Phascolarctos* from the Marmor and Mt. Etna deposits extend the northern geographic distribution of Pleistocene koalas from central eastern Australia (e.g., Price, 2008a) to northeastern central Queensland. Thus, the new koala records are important because they show that *Phascolarctos* has been closely associated with eastern Australian habitats since the Middle Pliocene.

Palaeoecology. The modern Koala, *Phascolarctos cinereus*, is mostly restricted to open forests and woodlands of eastern Australia (Moore & Foley, 2000), but has been recorded, albeit as a rare component, in rainforest communities (Williams *et al.*, 1996). Koalas are folivores and feed almost exclusively on the leaves of certain species of *Eucalyptus* (Moore & Foley, 2000). Thus, because fossil species of *Phascolarctos* such as *Ph. stirtoni*, have morphologically

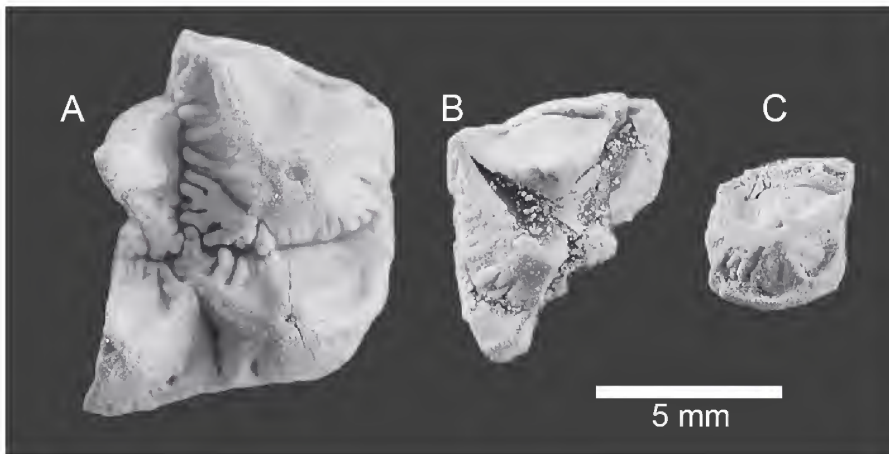


Fig. 4. Photographs of fossil koala teeth from eastern Australia. (A) QMF52288, LM² of *Phascolarctos* sp., site QML1384, Mt. Etna. (B) QMF52289, RM^{1, 2} or ³ metacone fragment of *Ph. ?stirtoni*, Chinchilla. (C) QMF52290, RM² protocone fragment of *Ph. ?stirtoni*, Marmor.

similar dentitions to *Ph. cinereus* (Bartholomai, 1968), the underlying assumption is that they had broadly similar habitat and dietary preferences (Archer *et al.*, 1991).

The Chinchilla Local Fauna represents a rich and diverse assemblage of fossil taxa, many of which are considered to be restricted solely to Pliocene deposits (e.g., *Euryzygoma*) (Archer, 1977b). The fauna includes molluscs, fish, lungfish, crocodiles, turtles, squamates, birds, rodents, dasyurids, bandicoots, diprotodontoids, wombats, marsupial lions, kangaroos, wallabies, and rodents (Bartholomai & Woods, 1976; Hutchinson & Mackness, 2002). The Pliocene palaeohabitat of the region was interpreted as consisting of a seasonal wetland component, with grasslands interspersed with complex and mature woodlands (Hutchinson & Mackness, 2002). The interpreted Pliocene habitat differs significantly from the habitats of the region today, which are dominated by open *Acacia* and *Eucalyptus populena* woodlands and grasslands (Fensham & Fairfax, 1997). Dawson (2004) recently described the first record of a potentially arboreal tree kangaroo from the assemblage. Thus, the identification of *Phascolarctidae* gen. et sp. indet. and *Phascolarctos ?stirtoni* significantly increase the known diversity of arboreal forms within the Chinchilla Local Fauna. Although the presence of such taxa provides support for the former existence of large-scale complex woodlands, they do not necessarily indicate Pliocene closed-forest in the region (Dawson, 2004). The modern Koala, *Ph. cinereus*, is extant in the region, whilst tree kangaroos are now restricted to rainforest communities in northeastern Queensland and New Guinea. Tree kangaroos are also absent from nearby intensively-sampled Late Pleistocene deposits of the eastern Darling Downs and Gore (Bartholomai, 1977; Price & Sobbe, 2005; Price & Webb, 2006; Price *et al.*, 2009). Generally, both the Late Pleistocene Darling Downs and Gore fossil faunas are dominated by terrestrial, non-arboreal, open woodland and grassland taxa (Bartholomai, 1977; Price, 2002, 2005; Price & Sobbe, 2005; Price *et al.*, 2005, 2009; Price & Webb, 2006) with very few species that also occur in Pliocene deposits (a possible exception being a species of marsupial “tapir”, *Palorchestes* (Price & Hocknull, 2005)). Thus, those data suggest that significant habitat and faunal reorganization occurred in the Chinchilla region between the Pliocene and Pleistocene, presumably reflecting the contraction of dense woodlands and expansion of open woodlands and grasslands. A local reduction in habitat heterogeneity (associated with an expansion of open habitats) is also evident between the Late Pleistocene and Recent

(Price & Sobbe, 2005). Therefore, those observations suggest that significant regional habitat changes have been underway since at least the Middle Pliocene.

The Middle Pleistocene Marmor (Site QML1420) faunal assemblage includes dasyurids, thylacinids, possums, marsupial lions, wombats, diprotodontoids, macropodoids, and rodents (Longman, 1925; Hocknull, 2005). The palaeohabitat is interpreted as representing a mosaic vegetation complex comprised of sclerophyll forest and grasslands based on the presence of closed forest taxa (e.g., tree kangaroos and pademelons) and open woodland taxa (e.g., grazing kangaroos and wombats) (Hocknull, 2005). The presence of *Phascolarctos ?stirtoni* supports an open woodland component of the Pleistocene habitat. The interpreted palaeohabitat differs from the modern habitat of the region, which is dominated by open woodlands and grasslands, with refugial forest and vine thickets restricted to the hillsides. Although some arboreal taxa such as tree kangaroos are now locally extinct, extant Koala populations persist in the region.

Site QML1384 (Mt. Etna, Unit “L.U.”) contains a diverse faunal assemblage including squamates, turtles, dasyurids, bandicoots, possums, kangaroos, bats, and rodents. Hocknull (2005) suggested that the palaeohabitat was an angiosperm-dominated rainforest based on the presence of “specialist” extant rainforest taxa such as cuscuses (*Strigocuscus*), striped possums (*Dactylopsila*), tree kangaroos (*Dendrolagus*), and giant white-tailed rats (*Uromys*). The new record of *Phascolarctos* sp. in the assemblage suggests the possibility that a more sclerophyllous open-forest habitat type was also sampled in the deposit. That interpretation does not necessarily refute the hypothesis that the palaeohabitat was predominantly rainforest, but it does suggest that *Eucalyptus* may have formed a minor vegetative component of the palaeohabitat. Thus, the Middle Pleistocene vegetation surrounding the QML1384 “L.U.” deposit may have consisted of a mosaic of habitat types. Such mosaic habitat types appear to be characteristic of many pre-Holocene Australian fossil deposits (Lundelius, 1983, 1989; Price, 2005). Alternatively, the deposit represents a significantly temporally-mixed assemblage. U/Th dating of the deposit (Table 1) provides only minimum ages of deposition and thus, the precise duration of accumulation cannot be determined. The provenance of fossil material is unclear. It is possible that different habitats occurred, and were sampled proximal to the cave over the period of deposition. However, this hypothesis cannot be tested on the basis of the data

Table 1. U-series isotopic data for eastern Australian fossil localities.

sample name	site	material	age interpretation		U (ppm)	^{232}Th (ppb)	$^{230}\text{Th}/^{232}\text{Th}$	$(^{234}\text{U}/^{238}\text{U})$	$(^{230}\text{Th}/^{238}\text{U})$	uncorrected ^{230}Th Age (ka)	corrected ^{230}Th Age (ka)	initial $(^{234}\text{U}/^{238}\text{U})$
			min. age	max. age								
ROK27 cal	QML1384 Lower Unit	calcite filling in bone	min. age	0.0822±0.0001	7.61	38.6	1.1777±0.0024	1.1795±0.0073	333±13	332±14	1.466±0.016	
ROK27 bone	QML1384 Lower Unit	macropod bone	min. age	4.6035±0.0048	15.14	1278	1.3991±0.0027	1.3856±0.0069	267±5	267±5	1.851±0.011	
ROK12	QML1420 Lower Unit	tooth	min. age	13.6008±0.0291	7.32	11583.8	2.4393±0.0037	2.0554±0.0085	153.8±1.3	153.8±1.3	3.226±0.008	
ROK12	QML1420 Lower Unit	calcite within tooth	min. age	0.0918±0.0001	33.16	13.4	1.8701±0.0053	1.5338±0.0299	152.3±5.7	147.8±10.9	2.461±0.055	
ROK13	QML1420 Lower Unit	tooth from breccia	min. age	1.8465±0.0010	1.37	3835.6	1.3342±0.0018	0.9391±0.0029	122.9±0.7	122.9±0.7	1.4735±0.023	

Note: Ratios in parentheses are activity ratios calculated from the atomic ratios, but normalized to measured values of secular-equilibrium HU-1 standard following the method of Ludwig *et al.* (1992). Errors are at 2σ level. ^{230}Th ages are calculated using Isoplot EX 2.3 (Ludwig, 1999) with decay constants $\lambda_{238} = 1.551 \times 10^{-10} \text{ yr}^{-1}$ (for ^{238}U), $\lambda_{234} = 2.835 \times 10^{-6} \text{ yr}^{-1}$ (for ^{234}U) and $\lambda_{230} = 9.195 \times 10^{-6} \text{ yr}^{-1}$ (for ^{230}Th), respectively. 2σ errors in the uncorrected ages were propagated directly from the uncertainties in the $(^{230}\text{Th}/^{238}\text{U})$ and $(^{234}\text{U}/^{238}\text{U})$. The corrected (corr.) ^{230}Th age was calculated assuming the non-radiogenic U-Th component with average upper crustal $^{232}\text{Th}/^{238}\text{U}$ atomic ratio of 3.8 ± 1.9 (^{230}Th , ^{234}U and ^{238}U are assumed to be in secular equilibrium). Such corrections have little impact on the ages.

currently available for site QML1384 (e.g., cave stratigraphy and dating). Regardless, the loss of Middle Pleistocene rainforests from both the Mt. Etna and Marmor regions, was likely the result of significant Middle Pleistocene climate change (Hocknull *et al.*, 2007). The local extinction of several arboreal rainforest mammals, and survival of the extant *Phascolarctos* since the Middle Pleistocene, further highlights the vulnerability of rainforest-associated faunas to vast climatic perturbations.

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Appendix. Modern *Phascolarctos cinereus* southeastern Queensland specimens examined.

registration number	location
QMJ13610	Yelarbon
QMJ15156	Jondaryan
QMJ8119	Yeronga
QMJ1350	Burleigh
QMJ992	10 miles W of Ipswich
QMJ64	Caboolture
QMJ4668	Caboolture
QMJ10972	Amberley
QMJ3404	Bribie Island
QMJ3793	Brisbane River, Bellevue
QMJ10034	Moggill
QMJ3835	Chinchilla
QMJ4370	Chinchilla
QMJ5749	Range near Brisbane
QMJ7118	Camp Mountain near Brisbane
QMJ14981	Cavern Pine Forest, Gold Coast
QMJ7240	Tamborine
QMJ8811	Toogoolawah
QMJ8353	West Burleigh
QMJ14982	Mt. Tamborine